USE OF SUCCESSIONAL HABITAT AND FRUIT RESOURCES BY SONGBIRDS DURING AUTUMN MIGRATION IN CENTRAL NEW JERSEY

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ABSTRACT.—We evaluated the effects of plant succession on habitat use and fruit resource availability for autumn migratory and resident songbirds in 43 ha of abandoned farm fields in central New Jersey. Using fixed net sites, standardized effort, and simultaneous sampling across habitat types, we mist-netted birds to compare habitat use and found that (1) use of three shrub-tree invasion interfaces declined as fruit-bearing shrubs were overgrown by trees, while use of three open shrublands changed little over the same period; (2) use of two pairs of contrasting successional habitats, shrubland and young woodland, was higher in the shrubland with abundant, highly nutritional fruits than in young woodland with sparse fruit; and (3) use of three shrublands at similar successional stages but with different fruit availability differed by bird taxonomic family and migratory strategy. Data on species composition and relative abundance of fruit-bearing shrubs and fruit consumption by birds (assessed by regurgitated and defecated matter) were used to elucidate avian patterns of habitat use. The relative abundance of fruit-bearing species may be more important than habitat structure in determining habitat use by birds. Shrubland dominated by panicled dogwood (*Cornus racemosa*) was favored over shrubland dominated by red cedar (*Juniperus virginianum*) or multiflora rose (*Rosa multiflora*). Favored vines were Japanese honeysuckle (*Lonicera japonica*), Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Toxicodendron radicans*), and grape (*Vitis* spp.). *Received 26 April 1999, accepted 29 Dec. 1999.*

Recently researchers on migratory songbird populations have emphasized the need for better knowledge of habitat and resource requirements during spring and autumn migration (Keast and Morton 1980, Hagan and Johnston 1992, Moore et al. 1993). Nearctic-Neotropical migrants require stopover habitats to amass stored fat to fuel their extended flights to wintering grounds in the West Indies and Central and South America. However, few researchers have explicitly examined food abundance or resource availability during migration to determine the most important stopover habitats for migratory birds, where such habitats occur, or how habitat distribution and abundance are changing as a result of development and land conversion (Moore and Simons 1992). Fewer researchers have examined habitat use in autumn migration (see Winker et al. 1992, Weisbrod et al. 1993, Parrish 1997, Yong et al. 1998). Autumn migrations of songbirds have been monitored for decades (see Baird et al. 1957, Eastern Bird Banding Association News 1969–1975, North American Bird Bander 1976–1999); however, detailed habitat data are not reported with bird capture data.

New Jersey straddles two important migratory flyways, the Atlantic Coast in the east and the Delaware River Valley in the west. The objective of this study in central New Jersey was to elucidate three questions concerning autumn migrant songbirds: which successional habitats do autumn migrants use most frequently, what are the effects of plant succession on use of these habitats, and what is the relationship between fruit availability and habitat use?

STUDY AREA AND METHODS

Study area.—The study site (40° 25' N, 74° 46' W) was located at 134 m elevation in the Sourland Mountains Piedmont physiographic province in Hopewell Township, Mercer Co., west-central New Jersey. The area consisted of 7 abandoned fields totaling approximately 43 ha: Fields 1–4 (each ca 6.5 ha) and Field 10 (1.8 ha). Fields 1–4 were last cultivated in 1959 but the center of Field 2 was plowed parallel to the net lane in 1978. Field 10 was last mowed in 1970. The fields are bordered by country roads, a woodlot, 11 houselots, and a forest tract of approximately 300 ha (Fig. 1, see Suthers 1988 for details).

Yearly vegetation surveys were initiated in 1977 (Suthers 1988). The habitat of each field was characterized by layers of vegetation (herb, shrub and tree), height, and percent of cover by each layer (James and

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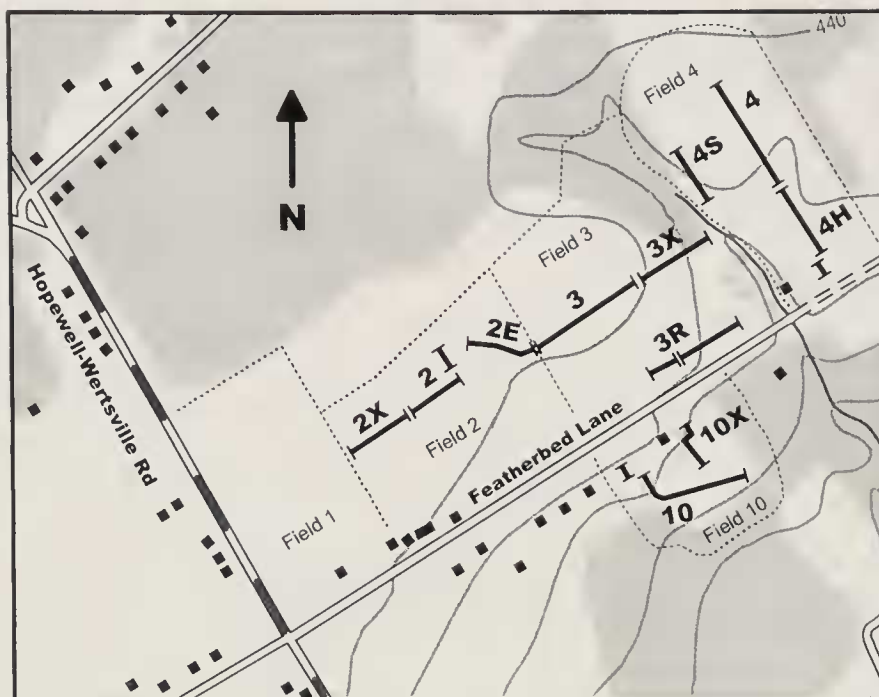
FIG. 1. Map of old fields in the study area showing fixed locations of mist nets superimposed on the 1954 USGS Topographic Map, Hopewell Quadrangle. The gray represents the extent of forest before the successional changes described in Suthers (1988) and in this paper. Contour intervals are 6.1 m (20 feet), the highest being 134 m (440 feet). Darkened squares are homes and barns. In comparisons of bird captures during long term successional changes, Lanes 2X and 10 were open shrublands, Lane 2 was an intermediate shrubland, Lane 2E was a shrub-tree interface, Lanes 10X and 3 were shrubland-tree invasions. In comparisons during short term contrasting stages, Lanes, 3, 3X, and northern portions of Lanes 4 and 4S were young woodlands and Lane 2, and southern portions of Lanes 4 and 4S were wooded shrublands. In comparisons of same stage, unequal fruit resources, Lanes 2, 3R and 10 were wooded shrublands, dominated by panicled dogwood, red cedar and multiflora rose/vines, respectively.

Shugart 1970, DeSante and coworkers 1993). Herbs were defined as grasses, sedges, rushes, forbs, and woody seedlings less than 0.5 m high, shrubs (including sapling trees) as woody plants 0.5–5 m tall, subcanopy as young trees and shrubs 5–10 m tall, and canopy as trees 10 m or greater.

Habitats were designated according to the successional stages surrounding the fixed net lanes at the time of the various comparisons. Open shrublands had about 30% cover up to 1 m high dominated by panicled dogwood (*Cornus racemosa*) or multiflora rose (*Rosa multiflora*), and 70% cover by grasses and forbs dominated by goldenrods (*Solidago* spp., *Euthania* spp.). Intermediate shrublands had about 50% cover over 1 m high that included a few scattered deciduous and red cedar (*Juniperus vrginianum*) saplings. Dense shrublands had about 85% cover up to 2.6 m high that included scattered saplings and vines at shrub height. Wooded shrublands had up to 75% shrub cover over 2 m high, dominated by panicled dogwood in Lane 2, red cedar in Lane 3R, and multiflora rose/vines in Lane 10, and 30–50% mixed deciduous tree cover up to 7–9 m high, that included various vine species that climbed up the trunks. Shrub-tree interface had 50% shrub cover of panicled dogwood 2 m high that interfaced with a dense invasion of 3 m high red maple (*Acer rubrum*) saplings and mixed hardwood seedlings. Tree invasions had 90% cover of mixed decid-

uous trees less than 9 m high that either preempted or shaded out shrubs and forbs. Young woodlands had 19% canopy cover up to 12 m high, 60% subcanopy cover up to 8 m high, 1–20% dwindling shade-intolerant shrub cover, and a sparse forb cover.

In autumn 1991–1993, species and abundance of fruit-bearing shrubs within 2 m of the net lanes were recorded. In September–October 1995–1997 fruit abundance and rate of disappearance was assessed on bird sampling days. In each lane fruits were counted on marked branches of 10 plants each of various species. Panicled dogwood ripened in mid-August and was available until mid-October. Autumn-olive (*Elaeagnus umbellata*), Virginia creeper (*Parthenocissus quinquefolia*), and frost grape (*Vitis vulpina*) fruits ripened in September and were consumed by late October. Multiflora rose ripened in late September, red cedar, poison ivy (*Toxicodendron radicans*), and Japanese honeysuckle (*Lonicera japonica*), ripened in October, and the fruits persisted into winter.

Bird surveys.—Bird abundance data were collected by mist-netting simultaneously in two or three fields of contrasting or similar vegetative structure in September–November, 1979–1997. The fields were transected with mist nets (12 m, 4 shelf, 30-mm mesh) set end to end in fixed sites, primarily oriented northeast-southwest (Fig. 1). There were 15 nets in Field 2 (Lanes 2, 2E, 2X), 26 nets in Field 3 (Lanes 3, 3X,

TABLE 1.   Comparisons of successional habitat use by fall migratory songbirds in September and October in central New Jersey piedmont.

Habitat	Lane	No. nets	Years operated	Days	Net hours	Birds
Long term successional changes						
Shrub-tree interface	2E	3	1979–1993 (no 1981, 1987)	40	667	286
Open shrubland	2X	4	1979–1983, 1992–1993, all simultaneously[a]	(16)[b]	803	554
Shrubland-tree invasion	10X	5	1982–1985	12	300	93
Open shrubland	10	5	Simultaneously	(12)	300	267
Shrubland-tree invasion	3	7	1984–1993 (not 1987, 1991)	(38)	1330	285
Intermediate shrubland	2	6	1979–1980, 1982–1983, then 1988–1993 simultaneously	53	1539	928
Short term contrasting stages						
Wooded shrubland	2 + 2X	7, 12	1989; 1992–1993	21	1110	582
Young woodland	3 + 3X	7, 12	Simultaneously	(21)	1110	149
Wooded shrubland	4 + 4S	4 + 3	1994	8	280	97
Young woodland	4 + 4S	4 + 3	Simultaneously	(8)	280	11
Fruit resources in three shrublands						
Dogwood dominated	2	7	1989–1991, 1995–1997	36	1260	568
Red cedar dominated	3R	7	Simultaneously	(36)	1260	428
Rose and vine dominated	10	7	Simultaneously	(36)	1260	579
				170	11,499	4827

[a] Nets were operated during the same years, days, and hours as the respective habitat being compared.
[b] Parentheses indicate number of days operated simultaneously with the habitat being compared.

3R), 23 nets in Field 4 (Lanes 4, 4H, 4S), and 15 nets in Field 10 (Lanes 10, 10X). Nets (20–32/day) were hung at daybreak one morning a week in the designated sites for comparison (Table 1).

Captured birds were collected every 30 min and placed in ventilated, individual compartments in holding boxes prior to processing. The net site of each capture was noted. Birds were processed within 30 min. They were identified and banded with U.S. Geological Service serially numbered bands. Data were taken on measurements, age, sex, weight, amount of fat in the furculum on a scale of 0–3 (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1977), and molt.

Because this was a study of habitat use by migrants and not temporal patterns of occurance during migration, capture data from weekly samples over 19 years were considered to be representative of habitat use patterns and smoothed from effects of yearly variations in vegetative growing seasons and weather. To document habitat use during successional changes over many years (long term), birds were captured in a shrub-tree interface and two shrubland-tree invasions as they succeeded to woodlands and in three slowly changing shrublands for comparison (Table 1). To determine whether birds preferred shrublands or woodlands, data were taken over a few years (short term) between two pairs of contrasting successional stages, wooded shrublands and young woodlands. To determine if there were shrubland preferences, habitat use was compared among three shrublands at similar suc-

cessional stages but with different dominating fruit resources: panicled dogwood, red cedar, or multiflora rose and vines.

There may have been a mist net bias in the wooded shrubland–young woodland comparisons because vegetation was shorter in the wooded shrublands and could have resulted in more effective sampling. However, the difference in height was small (1 m) and bias alone (Remsen and Good 1996) would not explain the large differences in capture rates. Birds were rarely observed foraging above the mist nets in the young woodlands, especially after hard frost in early to mid-October. Consequently, it was reasonable to assume that differences in captures during simultaneous sampling reflected abundance, that is, use of the habitat, rather than capture rate biases. Although there are inherent biases in mist net sampling, it is a useful and acceptable technique when done with field observations (Karr 1979, 1981; Remsen and Good 1996).

Fruit consumption survey.—In 1981–1982 and 1995–1997, after removing each bird from its compartment, any regurgitated or fecal matter was removed and all seeds found were identified by comparison with a reference collection gathered from the same locations. Field observations of fruit consumption also were recorded. Blake and Loiselle (1992) recommended fecal sampling because it was less biased than direct observation.

Data analysis.—The few (0.9%) birds recaptured from the previous season's annual breeding studies were considered to be using the habitat as autumn

birds, and were included in our analyses. November captures were considered to be migrants arriving to overwinter and were excluded from the analyses.

In the long term comparisons of successional changes, days of operation and net numbers in a habitat were not exactly matched with those of the shrubland habitat (Table 1). Therefore, data were standardized by using bird captures per 100 net hours (b/100 nh). Net hours were the number of nets $\times$ hours in operation (Karr 1981). Linear regression was used to examine the number of birds/nh for each habitat with itself each year. In the short term contrasting stages comparisons, and in the fruit resources comparisons the data were used from matched effort within and between years; therefore, the actual numbers of birds captured per day were used as the unit of analysis. Short term data over the years were pooled within each habitat type because they were similar based on linear regressions or Mann-Whitney U-test, all with $P > 0.05$. The pooling of short term years increased the samples and also assured that the bird catches were not peculiar to any particlar year of sampling. Short term use of the wooded shrublands and young woodlands were tested by the Mann-Whitney U-test. Pairs of categories, namely habitat use by family and by migratory strategy (Leck 1972, Robbins et al. 1989, Rappole et al. 1983), were tested by χ^2 with Yate's Correction. Differential use of shrublands with unequal fruit resources and categories of birds across these habitats were tested by χ^2. Abundance of fruit-bearing plants by habitat and the association of plant abundance with fruit eating birds and seeds recovered were tested by χ^2. Correlation between all fruit-eating bird species present and seeds recovered from ingested fruit was tested by Spearman Rank Correlation (r_s). Statistically significant differences were indicated at $P \leq 0.05$. StatView Student (Abacus Concepts 1991) package for the Macintosh computer and Statistics for Ornithologists (Fowler and Cohen 1995) were utilized for analyses.

RESULTS

In the 60 net spans and 11,499 net hr of effort used for the comparisons 4,827 birds of 93 species were captured during 170 weekly sample days in September and October 1979–1997 (Table 1). September was the peak of migrant species diversity (Suthers et al., unpubl. data); late October was the peak of migration (Leck 1972).

Bird use during long term successional changes.—Between 1979 and 1993 a shrub-tree interface (Lane 2E) succeeded into a young woodland. The number of birds captured in the interface ($n = 286$) declined significantly over time from 86 b/100 nh in 1979 to 8 b/100 nh in 1993 (linear regression: $R^2_{adj} = 0.33$, $F = 20.26$, 1 df, $P < 0.001$). By comparison, an open shrubland (Lane 2X) suc-

ceeded to dense shrubland and the number of birds captured ($n = 554$) did not change over time (50 b/100 nh in 1979 and 46 b/100 nh in 1993; linear regression: $R^2_{adj} = 0.0003$, $F = 1.01$, 1 df, $P > 0.05$).

Between 1982 and 1985 a black walnut (*Juglans nigra*) invasion of a multiflora rose shrubland (Lane 10X) had shaded out the shrubs and created an open understory with a shade tolerant forb cover. Bird captures ($n = 93$) declined significantly in the 4 years from 68 b/100 nh in 1982, to 4 b/100 nh in 1985 (linear regression: $R^2_{adj} = 0.61$, $F = 18.13$, 1 df, $P = 0.002$). In comparison, an open multiflora rose shrubland (Lane 10) expanded to a dense shrubland between 1982 and 1985 but the number of birds captured ($n = 267$) remained the same over the 4 years (104 b/100 nh vs 76 b/100 nh; linear regression: $R^2_{adj} = 0.23$, $F = 4.32$, 1 df, $P > 0.05$).

Between 1984 and 1993 a tree invasion shaded out a dense shrubland (Lane 3), forming a young woodland. Birds captured ($n = 285$) in the invaded shrubland declined significantly from 39 b/100 nh in 1984 to 7 b/100 nh in 1993 (linear regression: $R^2_{adj} = 0.135$, $F = 6.67$, 1 df, $P = 0.014$). In comparison, an intermediate shrubland (Lane 2) succeeded into a wooded shrubland and birds captured ($n = 928$) between 1979 (27 b/100 nh) and 1993 (31 b/100 nh) did not change (linear regression: $R^2_{adj} = -0.02$, $F = 0.06$, 1 df, $P > 0.05$).

Bird use of contrasting successional stages, short term.—In 1989 and 1992–1993 a wooded shrubland (Lane 2 above, including the dense shrubland extension Lane 2X) was compared with the young woodland (Lanes 3 and 3X above). Birds used the shrubland (582 captures) more frequently than the woodland (149 captures; $n_1 = 21$, $n_2 = 21$, $U = 36$, $P < 0.001$).

In 1994 a wooded shrubland (center Lanes 4 and 4S) and a young mixed deciduous woodland (north Lanes 4 and 4S) were compared. Birds used the shrubland (97 captures) more frequently than the woodland (11 captures; $n_1 = 7$, $n_2 = 7$, $U = 4.5$, $P = 0.01$).

Each taxonomic family had more birds in the shrublands than in the woodlands except Turdidae, which was similarly distributed (Table 2). Similarly when analyzed by migratory strategy, shrubland was used more often than

TABLE 2. Autumn migratory bird captures in shrublands and young deciduous woodlands in central New Jersey during 1989, 1992–1994. Captures are categorized by family and migratory strategy.

	Species	Shrubland captures	Woodland captures	χ^2
Family[a]				
Cardinalidae	3	27	3	19.20
Fringillidae	3	25	0	25.00
Emberizidae	8	141	2	135.11
Vireonidae	3	24	2	18.62
Parulidae	22	126	63	21.00
Mimidae	1	137	13	102.51
Regulidae	2	81	12	51.19
Paridae	3	50	16	41.76
Turdidae	5	36	28	1.00
Migratory strategy[b]				
Neotropical migrant	30	155	82	22.49
Short-distance migrant[c]	14	406	50	277.93
Permanent resident	8	116	28	53.78

[a] χ^2 tests, 1 df, $P < 0.001$ in all except Turdidae which were similarly distributed, $P > 0.05$.
[b] χ^2 tests, 1 df, $P < 0.001$, except the short-distance migratory Yellow-rumped Warbler which was distributed 10:10 in shrublands and woodlands and the Neotropical thrushes which were distributed 17:21, $P > 0.05$.
[c] Gray Catbirds (Mimidae) categorized here as short-distance migrants, could be considered Neotropical migrants.

woodland by Neotropical migrants, short distance migrants, and residents. Exceptions were four Neotropical migratory thrush species and short distance migratory Yellow-rumped Warbler (*Dendroica coronata*) that were equivalently represented in both habitats (Table 2).

Bird use of shrublands with disproportionate fruit resources.—Comparison of birds in three wooded shrublands (Lanes 2, 3R, and 10) resulted in 1575 captures of 35 families and 77 species (Table 3). Bird use was dissimilar. The panicled dogwood shrubland (Lane 2) was the most heavily used and the multiflora rose/vine shrubland (Lane 10) the least used by passage migrants during 1989–1991 ($\chi^2 = 31$, 2 df, $P < 0.001$). By 1995–1997 vines, most abundant in the multiflora rose/vine shrubland, had matured and fruited, and captures of passage migrants became equivalent in the multiflora rose/vine shrubland and the panicled dogwood shrubland, each higher than in the red cedar shrubland (Lane 3R; $\chi^2 = 10$, 2 df, $P = 0.006$). This change was mainly due to an influx of White-throated Sparrows (*Zonotrichia albicollis*) and Yellow-rumped Warblers in the multiflora rose/vines shrubland.

Although the short-distance migratory emberizids preferred the rose/vine shrubland (Table 3), the Eastern Towhee (*Pipilo erythroph-*

thalmus) was more abundant in the panicled dogwood shrubland ($\chi^2 = 7$, 2 df, $P = 0.03$). The Neotropical *Catharus* thrushes were not distributed differently ($\chi^2 = 2$, 2 df, $P > 0.05$), but the short-distance migratory Hermit Thrush (*Catharus guttatus*) was more common in the panicled dogwood shrubland ($\chi^2 = 8$, 2 df, $P = 0.019$). The Neotropical migratory Wood Thrush (*Hylocichla mustelina*) was more abundant in the rose/vine shrubland ($\chi^2 = 10$, 2 df, $P = 0.006$). Of the resident parids, the Tufted Titmouse (*Baeolophus bicolor*) favored the panicled dogwood shrubland ($\chi^2 = 22$, 2 df, $P < 0.001$), the Black-capped Chickadee (*Poecile atricapillus*) favored the red cedar shrubland ($\chi^2 = 14.11$, 2 df, $P < 0.001$), and the Carolina Chickadee (*P. carolinensis*) favored the rose/vines shrubland ($\chi^2 = 13.93$, 2 df, $P < 0.001$).

Defecated or regurgitated samples were deposited in the holding boxes by 431 birds of 77 species captured during 1995–1997. Evidence of fruit and seeds from ingested fruit was present in 333 samples (77%) from 42 species. Individuals of six additional species that were captured but left no evidence of eating fruit were observed eating fruit during the study. Altogether, 48 species (62%) of the 77 species captured had eaten fruit.

Equivalent numbers of individuals of the 42 fruit eating species were captured in the pan-

TABLE 3. Comparative mist-net captures in three wooded shrublands in central New Jersey with varying proportions of fruiting plant species. 1989–1991, 1995–1997. Dominant shrubs were panicled dogwood (*Cornus racemosa*) in Lane 2, red cedar (*Juniperus virginiana*) in Lane 3R, and multiflora rose (*Rosa multiflora*) in Lane 10.

	Birds captured			χ^2	P
	L2	L3R	L10		
Total captures 1575 birds	568	428	579	27.00	<0.001
Strategy					
Migrants, 1296 birds	470	343	483	27.70	<0.001
Residents, 279 birds	98	85	96	1.05	>0.05
Neotropical migrants, 7 families, 355 birds	131	89	135	10.98	0.004
Parulidae, 19 species	97	71	104	6.67	0.04
Turdidae[a], 5 species	13	9	17	2.46	>0.05
Vireonidae[b], 3 species	10	5	5	2.50	>0.05
Tyrannidae, 5 species	9	2	4	5.20	>0.05
Small samples combined: Cuculidae 2 sp., Trochilidae 1 sp., Thraupidae 1 sp.	2	2	5		
Short-distance migrants, 14 families, 941 birds	339	254	348	17.15	<0.001
Emberizidae, 7 species:	96	82	173	41.04	<0.001
Parulidae, 1 species[b]	33	42	35	1.22	>0.05
Mimidae[a], 2 species	106	52	56	25.38	<0.001
Troglodytidae, 2 species	7	5	14	5.15	>0.05
Regulidae, 2 species	52	46	50	0.38	>0.05
Turdidae[a], 2 species	28	20	12	6.40	0.04
Small samples combined: Scolopacidae 1 sp., Accipitridae 1 sp., Picidae 1 sp., Tyrannidae 1 sp., Certhiidae 1 sp., Vireonidae 1 sp., Icteridae 1 sp., Fringillidae 1 sp.	17	7	8	5.69	>0.05
Residents, 14 families, 279 birds	98	85	96	1.05	>0.05
Cardinalidae, 1 sp.	9	22	22	6.38	0.04
Emberizidae, 1 sp.	4	2	11	7.88	0.02
Paridae, 3 species	69	49	50	4.54	>0.05
Small samples combined: Strigidae 1 sp., Columbidae 1 sp., Picidae 3 sp., Bombycillidae 1 sp., Sturnidae 1 sp., Corvidae 2 sp., Sittidae 1 sp., Mimidae 1 sp., Turdidae 1 sp., Fringillidae 1 sp.	16	12	13	0.63	>0.05

[a] Primary frugivores.
[b] Secondary frugivores (see Blake and Hoppes 1986).

icled dogwood shrubland and rose/vines shrubland and fewer were captured in the red cedar shrubland (χ^2 = 25.10, 2 df, P < 0.001; Table 4). The number of species of fruit eaters did not differ by migratory strategy (χ^2 = 1.85, 2 df, P > 0.05). Most of the individuals were short distance migrants (χ^2 = 276.9, 2 df, P < 0.001), strongly represented by the Gray Catbird (*Dumetella carolinensis*), Yellow-rumped Warbler, and American Robin (*Turdus migratorius*).

Equivalent numbers of individuals of the 28 non-fruit eating species were captured in the panicled dogwood shrubland and the red cedar shrubland but more were captured in the mul-

tiflora rose/vine shrubland (χ^2 = 7.28, 2 df, P = 0.026). The highest number of non-fruit eating species were Neotropical migrants (χ^2 = 16.36, 2 df, P < 0.001). Neotropical migrants also had the most individuals (χ^2 = 87.54, 2 df, P < 0.001), strongly represented by warblers (Parulidae) with 13 species and 64 individuals.

The most frequent evidence of fruit consumption was recovered from Gray Catbirds (n = 86), Yellow-rumped Warblers (n = 55), American Robins (n = 41), Hermit Thrushes (n = 21), and White-throated Sparrows (n = 11), accounting for 67% of the positive samples. They took all of the 12 major fruit spe-

TABLE 4. The number of fruit-bearing plants next to the net lanes 1992–1997, and the average number of seeds recovered from 333 birds of 42 species that had eaten fruit, 1995–1997 in shrublands of similar successional stages in central New Jersey.

Plants	Fruit-bearing plants					Seeds ingested[a]		
	L2	L3R	L10	x^2	P	Lane 2	Lane 3R	Lane 10
Panicled dogwood *Cornus racemosa*	42	28	1	37	<0.001	0.6 Catbird 1**[b] Hermit Thrust 1***	0.1 Catbird 0.2	0.1 Catbird 0.2
Autumn-olive *Eleagnus umbellata*	5	22	1	8	<0.05	1 Catbird 1*** Robin 2	0.2 Catbird 1 Robin 0.2	0.1 Catbird 0.2 Cardinal 1**
Red cedar *Juniperus virginiana*	6	24	0	31	<0.001	0.01 Catbird 0.04	1 Robin 2***	0.1 Y-r Warbler 0.1
Multiflora rose *Rose multiflora*	30	26	112	84	<0.001	0.2 Mockingbird 1	1 Hermit Thrush 6***	0.4 Mockingbird 5
Virginia creeper *Parthenocissus quinquefolia*	4	2	2	1	>0.05	0.3 Gray-c Thrush 3	0.4	0.3 Hermit Thrush 1
Frost grape *Vitis vulpina*	1	1	24	41	<0.001	0.1 Catbird 0.1	0.2 Robin 1*	0.1 Robin 0.4***
Japanese honeysuckle *Lonicera japonica*	7	4	10	3	>0.05	0.1 Wood Thrush 2	0.2 Purple Finch 3	0.1 Y-r Warbler 2***
Poison ivy *Toxicodendron radicans*	1	1	4	3	>0.05	0.2 Y-r Warbler 1 W-t Sparrow 1	0.5 Hermit Thrush 3 Y-r Warbler 3 Purple Finch 3	1 Y-r Warbler 4*** W-t Sparrow 1
Other plant species	8	6	4	1	>0.05	0.5	0.2	0.1
Totals, all plants	97	111	150	12	<0.01			

Birds	Lane 2	Lane 3R	Lane 10
Total birds of 42 fruit eating species in each lane	135	68	130
Total birds eating shrub fruit	125	55	108
Number of shrub seeds recovered	194	126	78
Correlation (r_{Sp}) between birds and shrub seeds[c]	0.78***	0.77***	0.70***
Total birds eating vine fruit	104	63	119
Number of vine seeds recovered	84	96	387
Correlation (r_{Sp}) between birds and vine seeds[c]	0.56**	0.82***	0.78***

[a] Average number of ingested seeds recovered in a given lane, the species that ate the most, and the average number of seeds taken by that species. Species specific data on fruits taken by birds are available from the first author.

[b] P values, x^2 contingency coefficient of association, plant species abundance, bird species abundance, average number of seeds recovered.

[c] P values, Spearman's correlation coefficient (r_{Sp}) birds, average number of seeds recovered.

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

cies available. Purple Finches (*Carpodacus purpureus*, n = 5), Northern Cardinals (*Cardinalis cardinalis*, n = 13), and Tufted Titmice (n = 5) each took up to 10 species of fruit.

Fecal and regurgitated samples yielded up to four fruit species simultaneously in individual catbirds, up to three species of fruit in robins, and up to two species of fruit in Wood Thrushes and Hermit Thrushes. Virtually no insects were in samples from the primary frugivores, Gray Catbird and American Robin. A few insects were in samples with fruit from the *Hylocichla* and *Catharus* thrushes, Cedar Waxwings, Yellow-rumped Warblers, and Red-eyed Vireos (*Vireo olivaceus*). Insects mixed with some fruit were in samples from secondary frugivorous birds, Willow Flycatchers (*Empidonax trailii*), White-eyed Vireos (*Vireo griseus*), and Common Yellowthroats (*Geothlypis trichas*). Fecal samples that lacked fruit contained insect parts and/or undetermined pulverized matter (possibly seeds). Feces at daybreak, before birds could feed, were chalky.

The order, timing, and duration of fruit species consumed by birds agreed with observations of fruit availability. Fruit availability differed in the three shrublands (Table 4). In some cases there was a significant association between availability of a fruit species in a habitat, a bird species most numerous in that habitat, and the average number of seeds recovered from that bird (Table 4). Gray Catbirds in the panicled dogwood shrubland (55 samples) took 48% autumn-olive, 30% panicled dogwood, 12% multiflora rose, and smaller amounts of Virginia Creeper, fox grape, poison ivy and red cedar. Catbirds in the other two shrublands (31 samples) took 21% each autumn olive and multiflora rose, 15% poison ivy, 14% Virginia creeper, 12% panicled dogwood, 9% frost grape, and some Japanese honeysuckle and red cedar. Hermit Thrushes in the panicled dogwood shrubland (5 samples), took 56% panicled dogwood, 33% multiflora rose, and 11% autumn-olive. In the other shrublands (16 samples), they took 55% Japanese honeysuckle, 22% multiflora rose, 10% Virginia creeper, and smaller amounts of panicled dogwood, red cedar, frost grape, poison ivy and autumn-olive. The 4 Neotropical *Catharus* thrushes in the panicled

dogwood shrubland (12 samples) took 23% each of panicled dogwood and Virginia creeper, and 54% Japanese honeysuckle. In the other shrublands (3 samples) they took Virginia creeper and Japanese honeysuckle. Wood Thrushes in the panicled dogwood shrubland (5 samples), took 60% Japanese honeysuckle, 25% panicled dogwood, 10% autumn-olive, and 5% frost grape, and in the other shrublands (2 samples) took dogwood, autumn-olive and grape. House Finches (*Carpodacus mexicanus*) in the panicled dogwood shrubland (4 samples) took 67% autumn-olive and 33% poison ivy. White-throated Sparrows in the panicled dogwood shrubland (6 samples) and rose/vine shrubland (5 samples), took 44% and 31% poison ivy respectively, and 12% each of Virginia creeper and autumn-olive.

Yellow-rumped Warblers in the rose/vines shrubland (45 samples), took 59% poison ivy, and 38% Japanese honeysuckle. In the red cedar shrubland (7 samples) they took 88% poison ivy and smaller amounts of red cedar, Virginia creeper, and frost grape. American Robins (41 samples) in the red cedar and multiflora rose/vine shrublands took 46% red cedar, 29% Virginia creeper, 9% autumn-olive, 8% frost grape, and smaller amounts of multiflora rose, Japanese honeysuckle, panicled dogwood, and poison ivy. Cedar Waxwings (*Bombycilla cedrorum*) in the red cedar shrubland (3 samples) took 80% red cedar and 10% each frost grape and multiflora rose. In late October 112 birds of 20 species took 38% poison ivy, 28% grapes, 13% red cedar, and smaller amounts of viburnum, multiflora rose, silky dogwood, and crab apples.

DISCUSSION

Habitat use by birds in the autumn differed according to the successional stage and vegetative composition of the habitat. The successional habitat most frequently used by autumn migratory songbirds was shrubland. Vegetation structure was important, and birds abandoned shrub habitats that were shaded out by invading trees.

The abundance and/or quality of fruits appeared to be the resource that attracted migrants. If successional stage and vegetation structure alone were important in choosing between shrubland and woodland, birds would

have shown no preference among the three shrublands at similar successional stages; however, there was differential use of the shrublands. Not only did birds leave habitats as fruit-bearing shrubs became overgrown by trees, but they also increased their use of habitats as fruit resources increased. This influx of birds was seen especially in the increased use of the multiflora rose/vine shrubland as the vine fruits became available. The observation that autumn habitat choice was influenced by presence of fruit is consistent with the results of other studies. In a 600 ha forest plot 19 km NE from our study site, during an autumn Baird (1980) observed more birds and fruits along shrubby edges, clearings, and paths than in forest interiors. In central Illinois during 3 autumns Martin and Karr (1986) found more birds in forest light gaps with fruiting plants up to 3 m tall than in non-gap areas where vegetation cover up to 3 m had little fruit.

Only a few bird species captured in this study are not known to eat fruit. All but 6 of the captured 28 species lacking evidence of eating fruit have been shown to take some fruit, mostly in the autumn (Martin et al. 1951, Terres 1980, Ehrlich et al. 1988, Poole and Gill 1992, White 1989, Suthers 1988, Parrish 1997). The 6 species for which there is no evidence of fruit eating are Sharp-shinned Hawk (*Accipiter striatus*), Eastern Screech Owl (*Otis asio*), Ruby-throated Hummingbird (*Archilochus colubris*), Blue-winged Warbler, (*Vermivora pinus*), Worm-eating Warbler (*Helmitheros vermivorus*), and Winter Wren (*Troglodytes troglodytes*). With most species of small birds from many families taking fruit, it would seem that the trophic classification (Thompson and Willson 1979, Blake and Hoppes 1986) of most songbirds needs to be modified or qualified by season to include migration and winter diets.

As Hutto (1990) pointed out, it is hard to perceive food availability in the same manner as birds. Several factors possibly work together to explain why fruit resources should influence the choice of shrubland habitat. Birds shifted their diet with the changes in resource abundance from insects to fruit in September and October, based on fecal and regurgitated samples. Breeding season insectivores took fruit in the autumn even though arthropods,

especially Orthoptera, Diptera, and Arachnida were abundant until early to mid-October. The change from an insect diet to a primarily fruit diet was especially evident in the Gray Catbird, which was present until mid-October, and in the Yellow-rumped Warbler, present from October into winter.

Concurrent ripening and size limitations (see White 1989 for gape sizes) may determine which fruits are consumed together. Bird species for which we have larger sample sizes were eating almost every species of fruit available in the sequence that it ripened. Stiles (1980, 1993) and Bairlein and Gwinner (1994) demonstrated that frugivorous birds chose high lipid fruits first. Their studies did not include the introduced autumn-olive (1.4% lipids, 62.7% carbohydrates; nutritional data are from White 1989), a major source of carbohydrates in this study. It was eaten by many birds together with panicled dogwood (33.5% lipids, 22.1% carbohydrates), the most abundant source of lipids in this study. Nor did these researchers include the introduced Japanese honeysuckle (1.6% lipids, 50.3% carbohydrates) which was taken in large quantities together with poison ivy (42% lipids, 0 carbohydrates, Stiles and White 1986). White (1989) also found that lipid-rich and lipid-poor fruits were used concurrently, perhaps to achieve a nutritional balance (White and Stiles 1983).

Digestive availability is a crucial factor in how a bird utilizes food resources, and digestive ability may change seasonally with changes in the resources (Levey and Karasov 1992, Karasov 1996). In addition to Yellow-rumped Warblers, which are known to digest the waxy poison ivy fruits (Place and Stiles 1992), 20 other species also took poison ivy berries. There was no evidence from fruit samples or observations that Cedar Waxwings took high-lipid fruit, although they are capable of digesting lipids (Martinez del Rio and Restrepo 1993). The poorer ability of American Robins to absorb digested lipids compared to Wood Thrushes (Zurovchak et al. 1999) could explain why the robins were more plentiful in the red cedar shrubland and partook of Virginia creeper (16.2% lipids, 19.4% carbohydrates), together with red cedar (7.2% lipids, 41.7% carbohydrate), frost grapes (1.6% lipid, 47.9% carbohydrate), and multiflora rose

(1.5% lipids, 55.1% carbohydrates), whereas the Wood Thrushes, Hermit Thrushes and Swainson's Thrushes (*Catharus ustulatus*) partook heavily of panicled dogwood and high-carbohydrate fruit in the panicled dogwood shrubland. Digestive physiology could explain why flocks of birds visiting the frost grapes did not appear to ingest large amounts. The American Robin and Gray Catbird cannot digest sucrose (Martinez del Rio 1990, Malcarney 1992), but they seemed to take grapes as often as the Cedar Waxwing that can digest sucrose (Martinez del Rio et al. 1989, 1992). A digestive constraint in grapes may be phenolics that impair digestion. One suggested remedy is to mix grapes with arthropod protein (Witmer 1994). The mix of insects and fruit by the waxwing and thrushes is consistent with this hypothesis.

Age and experience may influence autumn frugivory because fruit is easier for the young to obtain than insects. Most (79%) of all birds we captured were young of the year. Fruits may determine habitat use by birds because of their need for rapid deposition of fat for migratory fuel. In the autumn, insect protein (over 70% dry weight; Robel et al. 1995) is thought to be less important to grown juvenile birds than the fruit lipids and carbohydrates needed for building fat deposits prior to migration (Stiles 1980, Bairlein and Gwinner 1994). Bairlein and Simons (1995) indicated that a combination of some protein with high lipid fruits may be optimal for digestive assimilation and fat accumulation. Only 10% of the migrants we captured, most of which were adults, appeared to have fat loads that would enable them to continue the next night without further refueling time (Blem 1980, Biebach et al. 1986). Most of the migratory birds we captured needed to amass fat. The average fat score, though only roughly correlated with amount of fat present, was 1.2 on a scale of 1–3, indicating insufficient fuel to support a long journey over the Atlantic Ocean (Moore and Kerlinger 1987).

Successional old fields with a diversity of native fruiting shrubs and vines are an important resource to autumn migratory birds that need to refuel for their long journeys. Winker and coworkers (1992) and Weisbrod and coworkers (1993) in Minnesota reported the heavier use of swamp, floodplain, willow and oak habitats, sedge fen, pine forest, and alder swale compared to upland forest habitats. Parrish (1997) reported the importance of fruiting scrub habitat for autumn migrants on Block Island off the coast of Rhode Island. These findings emphasize the need to conserve successional shrublands and other diverse habitats in addition to forests in the northeastern U.S. Birds also utilize the shrubs during spring migration and the shrubland attracts its own community of breeding migrants (Suthers 1988) that are declining because of loss of habitat (see Askins 1998 for overview). Land managers should consider maintaining and enhancing existing native fruiting shrublands and edge habitats to insure that these resources remain available.

ACKNOWLEDGMENTS

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